Atlas of comparative EMBRYOLOGY

Victor B. Eichler

ATLAS OF
COMPARATIVE EMBRYOLOGY

A LABORATORY GUIDE TO INVERTEBRATE AND VERTEBRATE EMBRYOS

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with 574 illustrations

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PREFACE

This atlas is a comprehensive laboratory guide to the structure of invertebrate and vertebrate embryos. It has been prepared to meet the need for a concise yet comprehensive guide for developing embryos, which are most often studied in undergraduate and graduate courses in developmental biology.

Although this book has been designed to supplement the study of whole mounts and serial sections of embryos in the laboratory, the photographs included are sufficiently representative to allow the student who has a limited amount of good material in the laboratory to learn the microscopic anatomy of these forms directly from this atlas.

This atlas was designed to incorporate the best features of similar guides now available, while making up for those features that are generally deficient or totally absent in this type of supplementary text. During the preparation of this atlas, efforts were principally directed toward thoroughness of presentation, while maintaining a format that would facilitate learning by the students. The results have produced a work unique among atlases insofar as it incorporates all of the following features.

It has been expanded to cover not only vertebrate material but also to include invertebrate forms whose development is of classical interest or that illustrate clearly a form of development generally discussed in developmental biology courses.

Large, well-labeled photographs are included in place of line illustrations or diagrams that often abound in laboratory guides.

The material was selected by developmental age (hours of incubation: chick embryos) or body length (in millimeters: frog and pig embryos) rather than by the tables of "normal" stages or somite number in the vertebrate species. The indices of development used here are by far the more standard for material purchased for courses in this country, although the latter may be the preferred designations in research studies.

All the stages that have generally been recognized as "most representative" for the development of the frog, chick, and pig are represented. Compared to these three groups, the fish and reptiles have been neglected

classes of vertebrates in terms of classroom study, but some, albeit limited, material is included for these groups for the sake of completeness.

Ample representative sections (transverse, sagittal, and frontal) are included, as well as whole mounts for the stages of development of the frog, chick, and pig. It is hoped that the many views provided by these photographs will enhance the student's understanding of these groups of animals.

There is abundant labeling of structures throughout the atlas. For the many representative serial sections of the frog and, particularly, the embryos of the chick and pig, where a large number of sections are provided, the structures are labeled with a number rather than with an identifying name. This procedure is believed to have at least two advantages: with the savings of label space, more structures can be identified, and students can test their knowledge of structures by attempting to identify each without the distraction of a printed name. The correct name for each numbered structure will be found in the Index to Structures in Section, which is located in a convenient foldout flap from the back cover.

A special consideration of the development of the vertebrate eye and teeth is included, respectively, in the coverage of chick and pig embryos.

The specimens of older chick embryos injected with black ink and subsequently cleared illustrate particularly well the vascular system of these important stages that would otherwise not be seen in whole mounts.

The human embryonic and fetal specimens, many with the embryonic membranes in place, are valuable supplementary material, which is often not available for examination in the laboratory.

A glossary of selected terms commonly encountered by the student using this book, as well as additional terms that are part of the basic vocabulary of the embryology laboratory, is included.

I would like to acknowledge the special contributions of Steve Harper, who expertly and conscientiously printed the final photographs; Steve Griffiths, who assisted me in photographing many of the large, opaque specimens; and Lee Mann and Gloria Louise Nusse, who each devoted much time and creative talent to the preparation of the cover and the five illustrations, respectively.

The National Aeronautics and Space Administration (NASA) provided the photographs of the developing fish embryos and gave permission to include them in this book.

With special gratitude I thank Sue and my friends, P. T., G. K., L. M., B. A., C. E., and S. A., who gave important measures of support during the completion of this project.

I also wish to extend my thanks to members of my comparative embryology classes who, by their interest in the laboratory material, guided my thoughts on what type of laboratory atlas could best serve their needs. It is my hope that this volume will meet the needs of future students of such courses and enhance their understanding of this subject.

Victor B. Eichler

The world is full of mysteries. Life is one.
J. B. S. HALDANE, 1966

INTRODUCTION

Embryology, very narrowly defined, may be regarded as the study of embryos—the stage of development of an individual while contained within the egg membranes. In viviparous mammals the embryo is the early developmental stage while contained within the embryonic and maternal tissues housing it, but before it begins to take on external features that make it identifiable as to species.

Generally, texts in embryology of animals cover, in addition to embryos per se, larval and fetal stages of development. Larvae are individuals that have hatched from an egg but look remarkably different from a small adult. The larval form generally has a radically different body form and life habitat than the adult. In Part Two several invertebrate larval forms are illustrated, and in Part Three the larval amphibian "tadpole" may be compared with the metamorphosed frog. Fetuses are generally regarded as young of viviparous mammals that have completed embryonic development and have taken on characteristics that make them recognizable as to the species to which they belong.

At least six separate processes are of interest to a broad study of animal embryology. The first three, **gametogenesis, fertilization,** and **cleavage,** are discussed and illustrated in Part One of this book. The latter three processes, **gastrulation, neurulation,** and **histological differentiation,** are the subject of the second and third parts of this volume.

It would perhaps be prudent to include here an explanation of the images that follow. All vertebrates, and many of the invertebrate species included in this book, have bodies that are bilaterally symmetrical, and thus three planes, each at right angles to the other two, may be defined (see the figure inside the front cover).

A cut through an embryo in the **sagittal plane** divides the animal into two sides—right and left. A thin section removed along the central axis in this plane is called a **median sagittal section;** any one not including the central axis is called a **parasagittal section.** A section cutting across the animal's body between the head and tail is made in the **transverse plane;** such sections are termed **transverse** or **cross sections.** Transverse sections are perhaps the most useful to study on microscope slides since they reveal the relationships

that exist in different structures within an embryo of any particular age and developmental changes that occur in the organ systems between embryos of different ages. A **frontal plane** divides the dorsal and ventral regions of an animal; a section in this plane is called a **frontal section.** A study of frontal sections is difficult in older animals as torsion and flexion of the body occurs, and sections in this plane are usually not studied beyond the very early stages of the establishment of the body.

Sections that are mounted on microscope slides that include every section in any plane are called **serial sections.** A set of serial sections is usually contained on several microscope slides, with sections mounted in rows that are viewed in order much as you read lines in a book—from left to right and top to bottom. Each section of a preserved embryo is sliced exceedingly thin, about 10 to 15 μ thick (1 μ = 1/1,000 mm); several areas of sections are mounted on a slide, stained with biological dyes to enhance the microscopic detail of the structures, and protected with a thin glass coverslip. Most of the photographs in this book were prepared from sets of serial sections of embryos that are typical of those used in laboratories of embryology or developmental biology courses, and it should be possible for you to use them to identify the structures viewed in your own class slides. Since they are fully labeled, it should even be possible to gain an understanding of the microscopic anatomy of the specimens without comparing them to actual material, if that is necessary.

Not every section from any set used for the photographs here has been included, but an interval of approximately 1:6 to 1:15 was selected, depending on the species and size of the embryo, with some deviation from a regular interval when it was desirable to include a section with an important structure that would otherwise be missed between sections. Hence the photographs of serial sections, where they appear, may be considered **representative** transverse, sagittal, or frontal sections rather than complete serial sets.

Perhaps the most difficult task for students of embryology is to learn to reconstruct a three-dimensional embryo from the essentially two-dimensional sections. Frequent study of the whole mount accompanying each section should assist in this task, and learning the positioning of major organs from sagittal sections before studying transverse sections is suggested. In the end, however, it requires persistence, dedication, and effort on the part of the student. No two embryos are exactly alike, and no set of sections is cut exactly like any other set; therefore it is important for the serious student to look at several sets to acquire confidence that he truly "understands" the arrangement of structures at any stage. Remember also that embryonic structures are continuously changing relative to each other during the embryonic period as development in a continuous process. Thus no chick embryo considered to have been incubated for 24 hours need be exactly the same developmental stage as another, nor are all pig embryos of 10 mm length exactly the same age or developmental stage. Knowing that such variations do exist

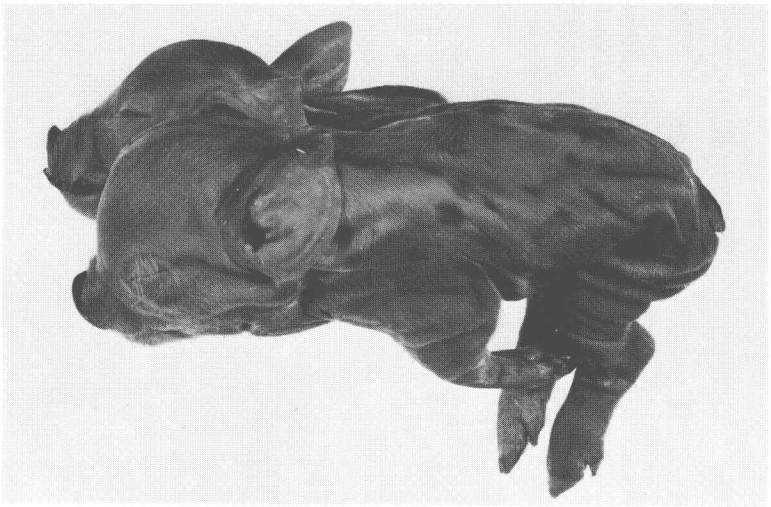
should be remembered by all students who pursue a study of embryos in section.

As you now begin your journey toward an understanding of the structures of embryos, as offered in this guide, I would like to offer the following thoughts of an eminent embryologist who 30 years ago wrote in the foreword of his text:

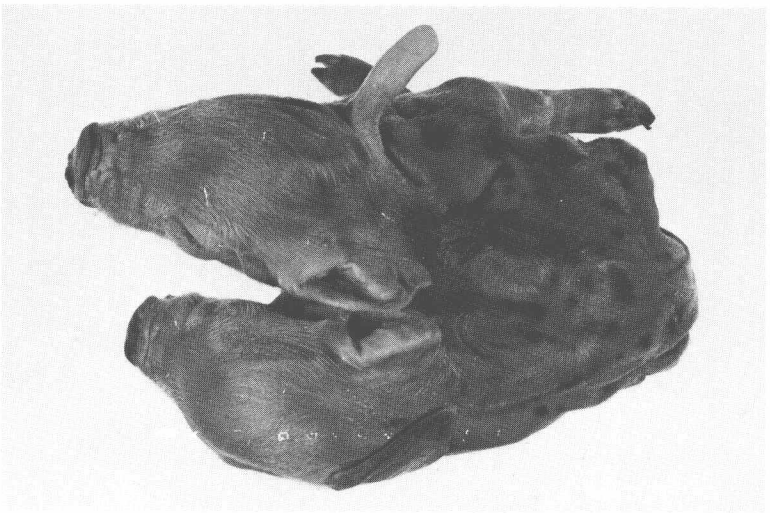
> You and I are to start out together to explore some of the regions of embryology. Still vivid memories of the erratic progress of my own first expeditions of that kind have led me to offer my services to you. Perhaps I can help you to avoid some of the difficulties I encountered and lead you to points of interest by routes less devious than you might otherwise find. But it is your own expedition. I am merely a guide. I can show you the passes to understanding but you must climb them. I can lead you to worth-while things but you yourself must unearth them and carry them away.*

With patience and disciplined study you can discover that your expedition may be a most rewarding and exciting one.

*From Patten, Bradley M.: Embryology of the pig, ed. 3. Copyright 1948 by McGraw-Hill Book Company. Used with permission of McGraw-Hill Book Company.



Two-headed pig, left lateral view



Two-headed pig, dorsal view

The marvelous thing to consider in the study of embryology is perhaps not that there are so many opportunities for development to go awry, but rather that it so regularly occurs normally.

CONTENTS

PART ONE

BASIC MECHANISMS

meiosis
fertilization
mitosis

The term "**meiosis**" refers to the process of cell division that reduces the diploid (2N) chromosome complement of a cell by half in the succeeding generation. Because mature gametes bearing a haploid (N) set of chromosomes are produced by meiotic cell division, meiosis is often referred to as a maturation or reductional process.

The entire process by which mature germ cells are produced (spermatozoon [pl., spermatozoa] in males; ovum [pl., ova] in females) is called **gametogenesis** and involves meiotic division as well as other maturational changes in both the nucleus and cytoplasm of the potential gametes. Gametogenesis in male animals is specifically called **spermatogenesis;** in females this process is known as **oogenesis** (see Fig. 1 for details).

On the following pages spermatogenesis is shown in the squash bug, an insect in the genus *Anasa*, and some of the maturational stages of oogenesis are shown for the roundworm *Ascaris*, which is a common intestinal parasite of pigs. Details of these processes are revealed particularly well in these forms, since the maturational stages appear in linear sequence from one end of the gonad to the other. Maturational stages of cells in the ovaries and testes of other invertebrate and some vertebrate species will be seen later in this book, where emphasis is more on morphology than the specifics of the processes.

Fertilization refers to a number of physical, chemical, and biological processes involving the attraction of the sperm to the egg, the penetration of the egg membranes and cytoplasm, and the union of the female and male pronuclei. The process of fertilization results in the formation of a **zygote,** or fertilized egg, capable of undergoing subsequent cell division to produce an independent, viable individual (Fig. 2). Each gamete formed by meiosis, the reductional division, has a haploid set of chromosomes. Thus their combining at fertilization will reestablish a diploid set of chromosomes in the zygote. The early stages of fertilization are illustrated in the sea urchin, *Arbacia;* the latter stages are shown in material of *Ascaris*.

The time of penetration of the spermatozoon varies in different groups of animals relative to the maturational state of the ovum. In some species sperm penetration may occur before the diploid germinal vesicle commences maturation; at the other extreme is the condition where meiosis is completed in the egg before sperm penetration occurs (Fig. 3).

Unlike the reductional process of meiosis, which occurs only in those cells of the ovaries and testes that are committed to producing gametes, **mitosis** is an equal process of cell division that can occur in any population of cells that maintains the capacity to increase in number. The first mitotic cell division occurs with the maternal and paternal chromosomes brought together in the zygote, and succeeding mitotic divisions occur in quite regular and often rapid succession throughout early cleavage stages of the developing embryo (Fig. 4). While mitotic cell division is responsible for increasing the number of cells in the embryo as early development rapidly progresses, it is not limited to the

embryonic period. Cells of many tissues, such as skin and the blood-forming tissues, retain the capacity to undergo mitosis throughout adult life.

Following mitotic cell division, each of the two daughter cells formed will have the same number of chromosomes and the same amount of genetic information as each other and as the original cell from which they were produced; hence, the diploid number of chromosomes will be preserved in all cells resulting from normal mitotic division. Stages of mitotic cell division are particularly clear in early cleavage stages of developing animals. The photographs included here are from the developing blastula of the whitefish, a fish of the genus *Coregonus*.

One difference between spermatogenesis and oogenesis is that the former results in four viable gametes following the first meiotic division, while the latter process favors one of the four potential gametes with the vast bulk of cytoplasm so one large female gamete (the ovum) and three small, nonviable polar bodies (polocytes) are produced. In any species all spermatozoa, ova, and polar bodies have the same number of chromosomes (one haploid set), although it has been found that in some species the first polar body may fail to divide, a feature that is of no consequence to the fertilizability of the ovum.

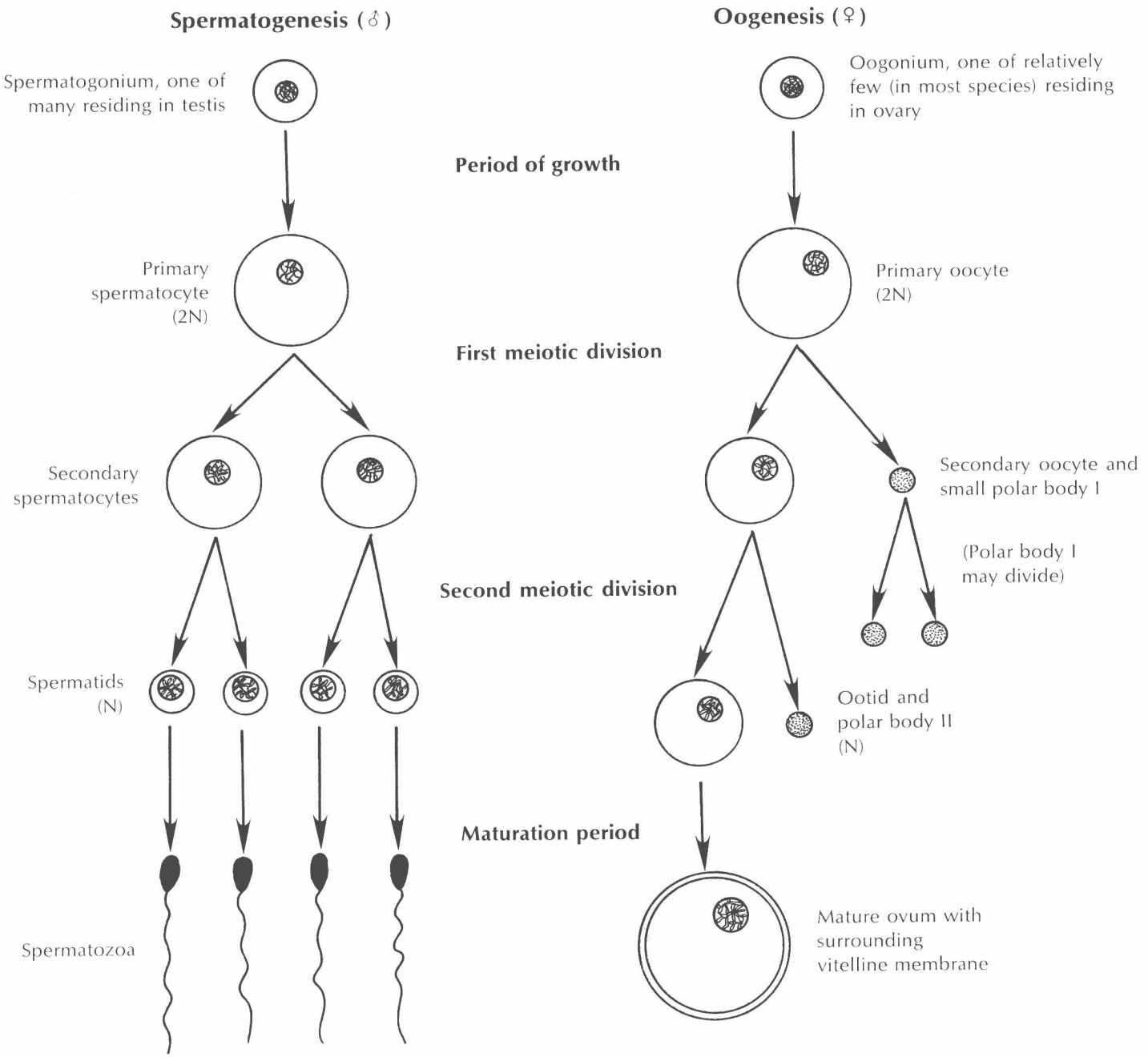


FIG. 1. Gametogenesis.

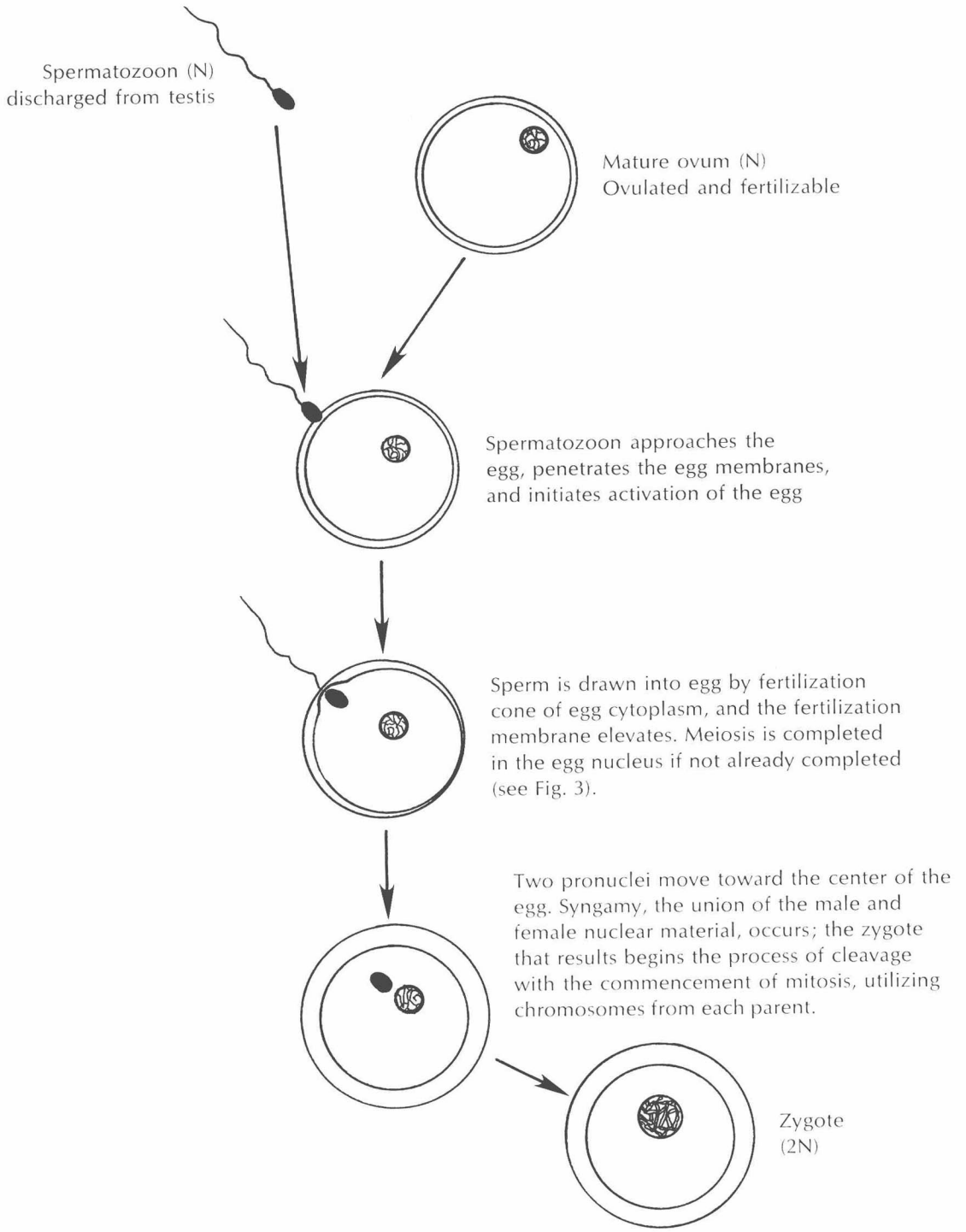
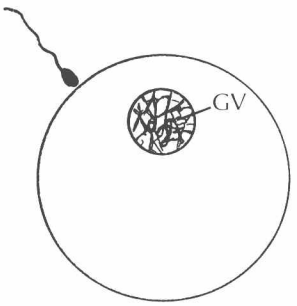
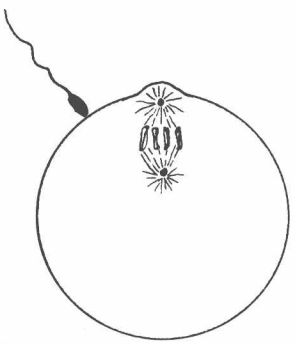


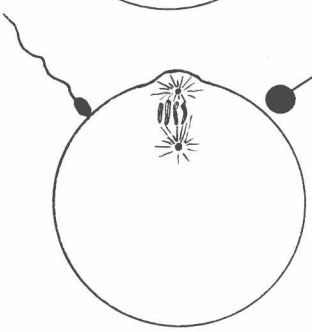
FIG. 2. Generalized schematic presentation of fertilization.



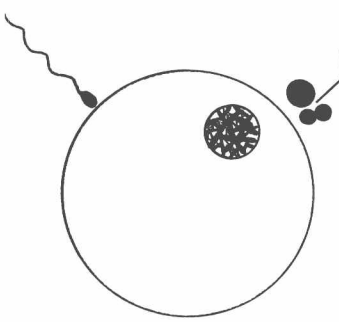
Sperm penetration before meiosis begins. The germinal vesicle (GV) is the immature female nucleus that is still diploid. Although the sperm nucleus enters the unripe egg, it remains inactive in the cytoplasm until the female nucleus completes meiosis and becomes haploid. Typical of the roundworm, *Ascaris*, and some annelid worms.



Egg maturation is arrested at the first meiotic metaphase until sperm penetration occurs, then meiosis proceeds. Typical of many annelids and molluscs.



The first meiotic division has been completed, a polar body (PB I) has been shed, and meiosis has proceeded to the second metaphase stage before the egg is penetrated by the sperm in most vertebrates, including humans.



After the process of meiosis has been completed and the second polar body (PB II) has been shed, fertilization is possible in such forms as the sea urchin, *Arbacia*, and most coelenterates.

FIG. 3. Time of fertilization relative to egg maturation.